Suitability for conservation as a criterion in regional conservation network selection

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Abstract The process of selecting candidate areas for inclusion in a regional conservation network should include not only delineating appropriate land units for selection and defining targets for representing features of interest, but also determining the suitability of land units for conservation purposes. We developed an explicit rating of conservation suitability by applying fuzzy-logic functions in a knowledge base to ecological condition and socio-economic attributes of land units in the interior Columbia River basin, USA. Suitability was converted to unsuitability to comprise a cost criterion in selecting regional conservation networks. When unsuitability was the sole cost criterion or was combined with land area as cost, only about one-third of the area selected was rated suitable, due to inclusion of unsuitable land to achieve representation of conservation targets (vegetation cover-type area). Selecting only from land units rated suitable produced networks that were 100% suitable, reasonably efficient, and most likely to be viable and defensible, as represented in our knowledge-based system. However, several conservation targets were not represented in these networks. The tradeoff between suitability and effectiveness in representing targets suggests that a multi-stage process should be implemented to address both attributes of candidate conservation networks. The suitability of existing conservation areas was greater than that of most alternative candidate networks, but 59% of land units containing conservation areas received a rating of unsuitable, due in part to the presence of units only partially occupied by conservation areas, in which unsuitability derived from conditions in non-conserved areas.

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Abbreviations

KB	Knowledge base
ECA	Existing conservation area
ICRB	Interior Columbia River basin
EMDS	Ecosystem Management Decision Support

Introduction

An important goal of regional conservation planning is establishing networks of conservation areas that represent the full range of biodiversity, expressed as a set of natural features (Pressey et al. 1993, 1996). Such representation must be achieved while satisfying potentially conflicting requirements, such as the need to minimize costs in the face of economic and social constraints, while also selecting areas for conservation that are suitable for the long-term maintenance of features of interest (Bedward et al. 1992; Possingham et al. 2000). The process of selecting candidate areas for inclusion in a regional conservation network includes delineating appropriate land units for selection, defining targets for representing features of interest, and determining the suitability of land units for conservation purposes. Several reserve selection algorithms have been developed to minimize costs while maximizing the representation of targets (Pressey et al. 1996, 1997; Csuti et al. 1997; Williams 1998; Possingham et al. 2000; Cabeza and Moilanen 2001; Margules et al. 2002; Cabeza et al. 2004; Williams et al. 2004). Cost measures have included number of units, land area, land price, and economic impact (e.g., Csuti et al. 1997; Ando et al. 1998; Wessels et al. 1999; Possingham et al. 2000; Stewart and Possingham 2005). Suitability for conservation has been explicitly incorporated into the selection process less frequently (Bedward et al. 1992; Stoms et al. 1998, 2002; Pyke 2005).

Suitability has been characterized and incorporated into the network selection process in several ways. Land-use suitability classes assigned to land units have been used to screen out unsuitable units in iterative selection algorithms (Bedward et al. 1992; Wessels et al. 2000) and have comprised constraints on selection in optimizing algorithms (van Lange-velde et al. 2000). Nantel et al. (1998) constructed a conflicting land-use potential index from several land-use potential, human population, and infrastructure variables. This index was used as a criterion for selecting land units in a heuristic algorithm. As part of a method for prioritizing sites as research natural areas in California, suitability indices for target vegetation types, calculated based on vegetation type area and environmental factors, constrained an optimizing selection algorithm (Stoms et al. 1998). The suitability of watersheds as potential biodiversity management areas was estimated for the Sierra Nevada Ecosystem Management Project (Davis et al. 1996). A watershed suitability index was calculated from a weighted sum of four factors: human population density; the fraction of the watershed affected by roads; the fraction of the watershed privately owned; and the degree of intermingling of public and private land. Selection of watersheds was accomplished by minimizing both area and suitability index as costs in a multi-objective model.

Davis et al. (1999) assigned suitability scores for conservation management based on land ownership, population density, road development, and proximity to core conservation areas to select a portfolio of candidate sites for The Nature Conservancy in the Columbia Plateau.

We characterized suitability using a fuzzy-logic knowledge base (KB) that quantifies contributions of environmental and land-use attributes to the suitability of land units for conservation (Bourgeron et al. to be submitted). This approach has value for assessing suitability when current knowledge exists about the relationships in a system, but in insufficient detail to construct an accurate mathematical model (Reynolds 2001). Fuzzy reasoning methods have been used to evaluate land suitability for crop and forest production (Hall et al. 1992; Davidson et al. 1994; Van Ranst et al. 1996; Groenemans et al. 1997; Kollias and Kalivas 1998; Ray et al. 1998; Ahamed et al. 2000; Triantafilis et al. 2001; Baja et al. 2002; Braimoh et al. 2004; Sicat et al. 2005), watershed condition (Reynolds et al. 2000; Dai et al. 2004) and conditions for forest sustainability (Reynolds et al. 2003). Several recent studies have incorporated fuzzy logic-based approaches to determine the suitability of land units for conservation or restoration. A suitability assessment was carried out to characterize sites as potential scientific research reserves for the University of California Merced campus using a fuzzy logic KB (Stoms et al. 2002). Pyke (2005) developed a fuzzy logic-based decision support system to evaluate the suitability of functionally-defined planning units for conserving the endangered California tiger salamander in Santa Barbara, California. In the eastern Washington Cascade Mountains, an analysis of departure of forest spatial patterns from reference conditions was implemented in a decision support system using fuzzy logic-based modeling, followed by a planning phase to assign restoration priorities (Reynolds and Hessburg 2005).

Objectives

Our objectives were to (1) assess the impact of introducing an explicit rating of conservation suitability into the process of producing regional conservation networks for specific targets of conservation, and (2) compare networks selected using suitability as a cost criterion with networks selected using other cost criteria and with existing conservation areas (ECAs), to determine how such networks differ in size, location, and representation of targets of conservation.

Methods

Study area

The study area (Fig. 1a) is the 58-million ha interior Columbia River basin (ICRB) in the northwestern United States. The ICRB extends east from the Cascade Crest in the states of Washington and Oregon to the continental divide of Montana and Wyoming, and incorporates a small portion of Utah and parts of the Klamath and Lahontan basins in Oregon and Nevada, respectively. The ICRB consists of mosaics of terrestrial and aquatic ecosystems as well as a variety of land-use and ecological conditions (Quigley and Arbelbide 1997). Elevation ranges from 20 to 4,200 m. The climate varies from hot and very dry in low elevation valleys and basins to temperate humid, with a strong maritime gradient from west to east, and high topographic relief in the mountain ranges (Reid et al. 1995).
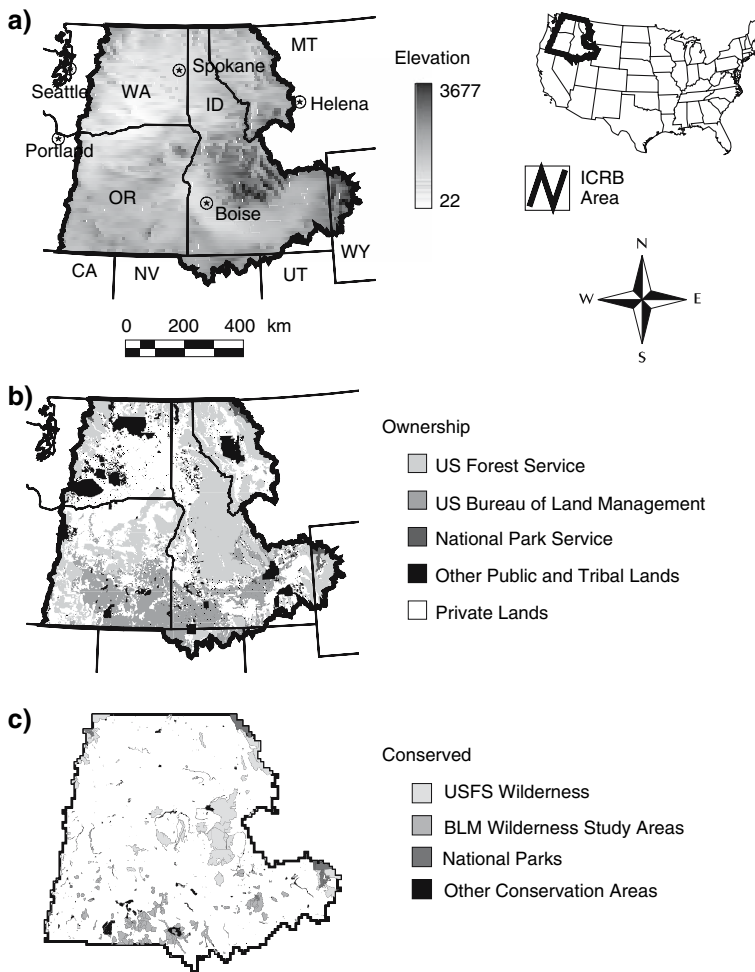
Fig. 1 Interior Columbia River basin study area in the Pacific Northwest, U.S. (**a**) Elevation and major cities; (**b**) land ownership classes, (**c**) conserved areas

Heterogeneity in environmental conditions in the ICRB is reflected in the diversity of its ecosystems, ranging from desert grasslands and shrublands to cold, wet forests and alpine vegetation. Mountainous areas comprising the Cascades and Rocky Mountains have predominantly maritime climates and support forest types such as cedar/hemlock (*Thuja plicata*/*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*). The intermountain area between the Cascades and Rocky Mountains has a semi-arid climate and is composed primarily of plains, tablelands, and plateaus, supporting sagebrush (*Artemisia* spp.) steppe and grasslands. Landscape diversity occurs at many spatial scales.

A large area of the ICRB (62%) is in federal, state, and tribal ownership; fifty-three percent is National Forest or is administered by the Bureau of Land Management (Fig. 1b; Quigley and Arbelbide 1997). Many low- to mid-elevation areas have been heavily impacted by grazing, agricultural, and urban land uses. Higher-elevation forested areas

have experienced changes in ecosystem processes resulting from fire suppression, effects of insects and disease, and timber harvesting. Approximately 12% of the ICRB has status as a conservation area; i.e., is designated as a U.S. Forest Service Wilderness, Bureau of Land Management Wilderness Study Area, National Park, or other conservation area, such as Research Natural Areas, Fish and Wildlife Natural Areas, Areas of Special Environmental Concern, Special Interest Areas, Wild and Scenic Rivers, and The Nature Conservancy preserves (Fig. 1c; Gravenmier et al. 1997). Land owned by the U.S. Forest Service, Bureau of Land Management, and National Park Service comprises more than 90% (52.5, 32.5, and 6.7%, respectively) of these ECAs. Although ECAs are found over a range of elevations in the ICRB, they occupy a disproportionately large percentage of high elevation areas (e.g., 30% of the land above 2,000 m in elevation is located in a designated conservation area, but only 2% of land below 500 m is conserved).

Conservation planning units and targets

We constructed conservation planning units for regional network selection by first clustering climate, hydrological, and biogeochemical variables into 37 biophysical classes that represent environmental gradients in the ICRB and that were tested for their performance in representing variability in biotic and abiotic attributes (Bourgeron and Humphries in revision). These units were further stratified by regional potential vegetation, an expression of the biophysical environment widely used for landscape analyses in the ICRB (Reid et al. 1995; Hann et al. 1997; Jensen et al. 1997). The resulting land polygons (Fig. 2; hereafter polygons) are intended to represent functional landscapes (Poiani et al. 2000); i.e., land areas whose boundaries enclose ecological patterns and processes expected to respond similarly to management or other perturbations (Bourgeron et al. 2001). A total of 17,227
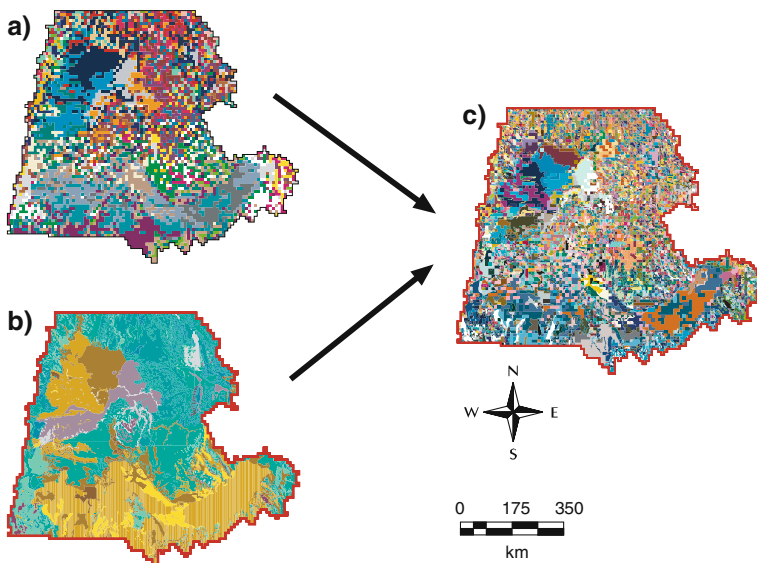

Fig. 2 Overlay of (**a**) ecological land units, and (**b**) potential vegetation, to delineate (**c**) biophysical environment polygons as conservation land units

polygons were delineated, representing 686 biophysical classes. Polygons ranged from 3 to 6,943 km^2, averaging 32 km^2 in size.

The conservation planning units set the spatial context for the protection of specific conservation targets. The complexity of biodiversity, at scales of organization from the individual to the ecosystem, requires the use of surrogate measures of biodiversity (Margules and Pressey 2000; Sarkar et al. 2006). At a regional scale, coarse-level biodiversity surrogates, such as species assemblages, habitat types, vegetation types, and land types are more likely to be widely and consistently available than finer-level surrogates and may better integrate the ecological processes that drive biotic distributions and ecosystem function (Margules and Pressey 2000; Fairbanks et al. 2001). Such surrogates have been prescribed as the targets of protection activities, such as representation of ecosystems in Research Natural Areas by the U.S. Forest Service (USDA Forest Service 1992; Snyder et al. 1999). However, this coarse-filter approach will not meet the needs of some fine-scale or taxonomically-based biodiversity features (Noss 1987; Csuti et al. 1997; Pressey 2004; Sarkar et al. 2006) that require comprehensive species data (Brooks et al. 2004). For the objectives of this study, the use of broad scale attributes was appropriate. Therefore, we used vegetation cover types (hereafter, cover types) as example targets of conservation in our analyses to demonstrate incorporation of suitability into conservation network selection. The targets of conservation were 35 naturally vegetated cover types derived from an existing database developed from 1 km-resolution Advanced Very High Resolution Radiometer data (Hann et al. 1997).

Knowledge-based application framework

To meet our first objective, we used a GIS-based integrated application framework, the Ecosystem Management Decision Support (EMDS) system, to construct and evaluate KBs to determine the conservation suitability of conservation planning units (Fig. 3; Reynolds 1999a). KBs describe logical relationships (dependencies) among ecosystem states and processes of interest. NetWeaver software was used in EMDS to develop KBs as interconnected dependency networks that represent hypothesized relationships of ecosystem states and processes to the suitability of conservation planning units (Reynolds 1999b). NetWeaver's object-based representation of dependency networks confers modularity on KB structure, allowing complex KBs to be easily constructed from simpler components. Dependency networks at lower levels are linked by relational nodes to generate higher-level states in the KB. Each dependency network in a KB is designed to test a proposition concerning an ecosystem state or process; for example, that the density of roads in a polygon is sufficiently low for conservation purposes. Networks ultimately terminate in data links, in which a polygon attribute is compared to a fuzzy-logic function, a quantitative representation of a proposition, to derive a suitability rating for each polygon that expresses the degree to which the proposition is supported by the data for that polygon. Suitability ratings range from –1 (proposition is completely false) to 1 (proposition is completely true). A suitability rating of 0 is designated as undetermined, indicating lack of evidence for or against the proposition. Polygon attributes and their associated KB propositions are described in Table 1. For example, the evaluation of the proposition that road density was low enough for conservation purposes was based on the distribution of road densities in polygons. A suitability rating of 1 (completely true) was assigned to a road density of 0 km/km^2, a rating of 0 (undetermined) to a density of 0.9 km/km^2, representing the 25th percentile of the distribution of road densities, and a rating of –1 (completely
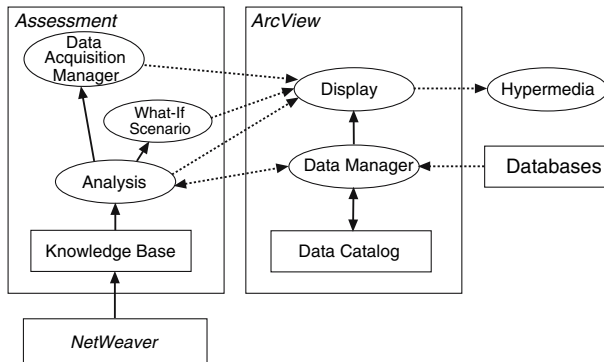
Fig. 3 Components of Ecosystem Management Decision Support application framework. Compartment labeled 'Assessment' comprises the knowledge base (KB) and subsystems (enclosed in ovals) that process the KB. Compartment labeled 'ArcView' represents the geographic information system controlling management and display of spatial data, including input and output from the KB (adapted from Reynolds 1999a)

false) to a density of 2.7 km/km^2, representing the 75th percentile of the distribution. Linear functions determined suitability ratings between these values.

Our KB model produced suitability ratings for polygons based on their overall ecological conditions (Bourgeron et al. to be submitted). Suitability was a function of polygon size and conditions, as well as conditions in a neighborhood surrounding the polygon (Fig. 4). A fuzzy-logic function applied to polygon size illustrates the evaluation of this polygon attribute to derive suitability ratings using threshold parameters of 20, 40, and 100 (Fig. 4). Sizes ≤ 20 km^2 received a suitability rating of –1 (completely false), sizes = 40 km^2 received a suitability rating of 0 (undetermined), and sizes ≥ 100 km^2 received a suitability rating of 1 (completely true). Linear functions determined the suitability rating between 20 and 40 km^2 (partial negative suitability) and between 40 and 100 km^2 (partial positive suitability). Threshold parameters for all fuzzy logic functions are given in Table 1.

If a polygon was sufficiently large, the suitability rating was considered to depend only on attributes of the polygon itself, without consideration of its neighborhood. Polygon suitability was judged to be a function of fuzzy-logic networks we termed defensibility (i.e., compatibility of land use with conservation activities), and viability (i.e., the likelihood that ecological conditions allow persistence of conservation targets). Defensibility was derived from a fuzzy-logic function applied to land use condition. Viability was assessed by fuzzy-logic functions applied to road density and degree of departure of current vegetation and disturbance regimes from historical conditions. Neighborhood suitability was evaluated with the same dependency networks as polygon suitability, but the fuzzy-logic functions were applied to the attributes of the polygons that adjoined the focal polygon.

The processing of a KB (termed an assessment in EMDS) is conducted in a GIS environment (ArcView), in which a catalog of polygon attribute data is assembled, the spatial extent is defined, and maps, tables, and graphs of results are displayed (Fig. 3). EMDS contains a scenario subsystem for performing 'what if' analyses by modifying input data or KB structure. In addition, a data acquisition manager subsystem can generate information concerning the influence of missing data on the results (Humphries et al. in revision).

Table 1 Polygon attributes, KB propositions, and threshold parameters of fuzzy logic functions evaluated to produce suitability ratings

Attribute	Description	Proposition	Fuzzy logic function threshold parameters		
			False (−1)	Undetermined (0)	True (+1)
Land use condition	Percent of polygon with light to moderate human impact.	Land use condition is acceptable for conservation purposes.	10	25	50
Road density	Km of roads/km².	Road density is low enough.	2.67	0.93	0
Disturbance change index	Percent of polygon with acceptable index of change in disturbance regime from historical to current.	Disturbance change is acceptable for conservation purposes.	1	5	50
Vegetation change index	Percent of polygon with acceptable index of change in vegetation from historical to current.	Vegetation change is acceptable for conservation purposes.	1	5	50
Polygon size	Area in km².	Size is large enough to allow operation of processes.	20	40	100
Polygon size	Area in km².	Size is so large that neighborhood suitability need not be evaluated.	100	125	150

Operation of an example fuzzy logic function with threshold parameters illustrated in Fig. 4

Fig. 4 Structure of knowledge base dependency networks (enclosed in ovals) terminating in data links (enclosed in rectangles), in which polygon attribute values are evaluated with fuzzy logic functions to derive suitability ratings. Statements in data link rectangles represent propositions regarding ecosystem state and processes tested by fuzzy logic functions
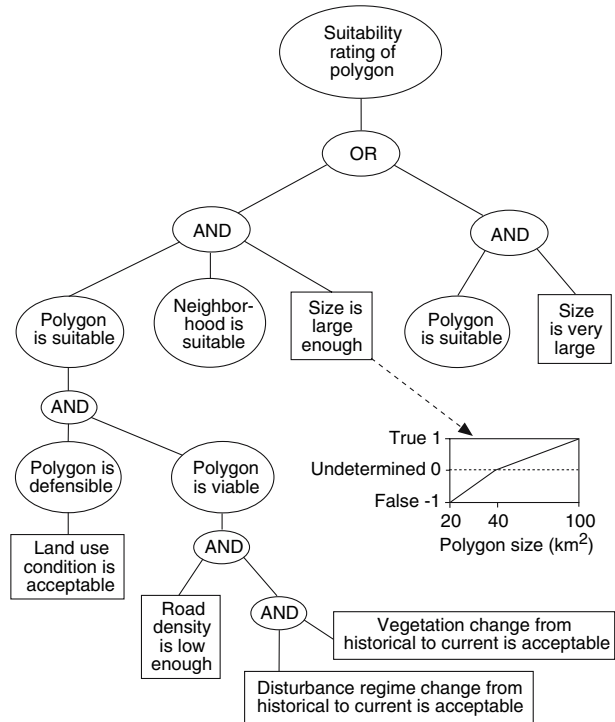
Conservation network selection

Polygons were selected as candidate members in conservation networks using Sites 1.0, a site selection toolbox implemented in ArcView, which uses a simulated annealing algorithm as a heuristic method for efficiently selecting representative sets of areas (Andelman et al. 1999). Simulated annealing is widely recognized as a preferred algorithm for iterative site selection, especially for large problems such as ours (Pressey et al. 1997; Possingham et al. 2000; McDonnell et al. 2002; Westphal and Possingham 2003; Oetting et al. 2006; Sarkar et al. 2006; but see Kelley et al. 2002; Fischer and Church 2005). The algorithm attempts to minimize the cost of a network while meeting goals for representing targets of conservation. Simulated annealing is a minimization method that iteratively makes additions and deletions to an initial randomly-generated or user-specified reserve network (Possingham et al. 2000). The algorithm avoids getting trapped in local optima by allowing exploration of a number of different routes by which a global optimum can be reached. Over time in a run, the algorithm becomes more and more selective about changes, accepting only those that decrease the cost of the network.

A good solution to the problem of selecting a conservation network is considered to be one in which the cost of the network is minimized, but as many targets of conservation as possible are included (Pressey et al. 1993; Possingham et al. 2000). To meet our second objective, we implemented 15 cost scenarios to evaluate the effect of different cost measures on network selection, and compared the resulting networks to ECAs (Table 2). The scenarios were designed to evaluate the use of our measure of conservation suitability as a cost criterion alone and in combination with other cost criteria. Scenarios 1, 2, and 3, were based on equal cost for all polygons, total area within a polygon as cost, or private

Table 2 Fifteen cost scenarios for selection of networks of candidate conservation areas compared to existing conservation areas in the ICRB

Scenario	No. of cover types present	No. of land polygons selected	Area selected (% of study area)	Mean polygon area (standard deviation)	Area selected that is suitable (% of selected area)	Percent of all suitable area selected
1	35	82	54,078 (9.7)	659.5 (1271.2)	3,070 (5.7)	5.7
2	35	3,087	30,113 (5.4)	9.8 (16.4)	2,006 (6.7)	3.7
3	34	1,417	36,558 (6.5)	25.8 (42.5)	7,823 (21.4)	14.6
4	35	131	45,237 (8.1)	345.3 (760.9)	15,358 (34.0)	28.6
5	35	128	45,260 (8.1)	353.6 (769.1)	14,769 (32.6)	27.5
6	35	128	45,461 (8.1)	355.2 (768.7)	15,027 (33.1)	28.0
7	35	124	50,128 (9.0)	404.3 (902.3)	14,558 (29.0)	27.1
8	35	127	50,269 (9.0)	395.8 (892.1)	15,084 (30.0)	28.1
9	31	242	28,807 (5.1)	119.0 (119.0)	28,807 (100.0)	53.7
10	34	2,574	73,075 (13.1)	28.4 (165.8)	27,311 (37.4)	50.9
11	34	1,839	48,999 (8.8)	26.6 (151.9)	15,784 (32.2)	29.4
12	35	99	54,292 (9.7)	548.4 (1224.5)	4,132 (7.6)	7.7
13	34	867	66,481 (11.9)	76.7 (421.6)	7,518 (11.3)	14.0
14	31	298	32,247 (5.8)	108.2 (203.8)	32,247 (100.0)	60.1
15	31	392	39,250 (7.0)	100.1 (183.5)	39,250 (100.0)	73.1
ECAs	33	4,117	65,371 (11.7)	119.0 (30.0)	26,523 (40.6)	49.4

Scenarios: 1, equal costs; 2, total polygon area as cost; 3, private land area in polygon as cost; 4, private land and unsuitability as cost in 1 to 1 ratio; 5, total area and unsuitability as cost in 1 to 1 ratio; 6, total area and unsuitability as cost in 2 to 1 ratio; 7, total area and unsuitability as cost in 1 to 2 ratio; 8, unsuitability as cost; 9, unsuitability as cost, selecting from suitable polygons only; 10, scenario 4 with polygons at least 50% conserved as seeds; 11, scenario 4 with 100% conserved polygons as seeds; 12, scenario 4 with boundary length modifier = 1; 13, scenario 4 with boundary length modifier = 10; 14, scenario 9 with boundary length modifier = 1; 15, scenario 9 with boundary length modifier = 10; ECAs, existing conservation areas. Area in km^2

land area within a polygon as cost, respectively. All other scenarios incorporated suitability ratings into the measure of the cost of the network. However, because cost is a quantity that is minimized in the algorithm, suitability must be converted to unsuitability to be used as a cost, producing a network in which unsuitability for conservation is minimized. Therefore, polygon suitability ratings derived from KBs were converted to unsuitability ratings by reversing their sign. These reversed sign ratings were then rescaled by adding one and multiplying by 5,000 to range from 0 to 10,000, approximating the magnitude of individual polygon areas, which ranged from 3 to 6,943 km^2. Scenario 8 was based on this cost measure. Scenario 9 was also based on unsuitability as cost, but selection was restricted to only those polygons with positive suitability ratings in the original NetWeaver scale of [–1, 1]. Additional cost measures were constructed by combining unsuitability with either total area or private land area.

We examined the effect of different weights of total area and unsuitability by combining them in ratios of 2 to 1 (scenario 5), 1 to 1 (scenario 6), and 1 to 2 (scenario 7). We also combined private land area and unsuitability in a 1 to 1 ratio (scenario 4). We implemented two scenarios in which ECAs comprised 'seeds' for network selection, using the combination of private land area and unsuitability as the cost measure. In one of these scenarios (10), polygons whose area was at least 50% conserved were fixed in the network, and those with conserved area less than 50% were included in the initial (seed) network but could be removed during a run. In another scenario (11), polygons that were 100% conserved were fixed in the network, and those that were at least 50% but less than 100% conserved were considered as initial seeds of the network subject to possible subsequent removal. Finally, we implemented four scenarios in which the spatial contiguity of network sites was constrained by minimizing total network boundary length (Andelman et al. 1999). Two boundary-length multipliers were used: moderate aggregation of polygons (boundary-length multiplier = 1), and high aggregation of polygons (boundary-length multiplier = 10). For each boundary-length multiplier value, scenarios were implemented for (1) cost as private land area and unsuitability combined (scenarios 12 and 13), and (2) restriction to suitable polygons only (scenarios 14 and 15).

Our goal in each analysis was to represent a certain percentage of the total area occupied by each cover type in the network; this percentage ranged from 5% for widespread cover types to 20% for infrequent cover types. The method of selection was adaptive simulated annealing with iterative improvement. For each cost scenario, ten runs of 100,000,000 iterations each were conducted and the run with the best result (lowest cost while attempting to meet area targets for cover types) was selected.

We evaluated the performance of scenarios and ECAs in representing cover-type areas by computing effectiveness, measured as the gap in representation between the desired target areas and those actually included in a network (Rodrigues et al. 1999). For each cover type i, the gap$_i$ in representation is:

$$\max \left[0, \frac{RTreq, i - RTnet, i}{RTreq, i} \right]$$

in which $RT_{req,i}$ is the representation target required for cover type i, and $RT_{net, i}$ is the actual amount included in the scenario or ECA network. Effectiveness is evaluated as:

$$1 - \frac{\sum_{i=1}^{m} gapi}{m}$$

ranging from 0 (no cover types reached their targets) to 1 (all cover types reached their targets), in which m is the number of cover types.

We calculated the efficiency (*sensu* Pressey and Nicholls 1989) of scenarios and ECAs as:

$$1 - \left[\frac{\text{network area}}{\text{total area}} \right]$$

Results

Selection of regional networks of candidate conservation areas

The number of polygons selected for inclusion in regional conservation networks varied widely among scenarios (Table 2). A small number of relatively large polygons were chosen in scenarios in which cost was equal among polygons (scenario 1) or cost included unsuitability but no network seeds were specified (scenarios 4–8 and 12). Somewhat smaller polygons were selected in scenario 9 (selection from suitable polygons only) and scenarios 13–15 (three of the four spatial aggregation scenarios). Networks containing many small polygons were generated using area as cost (scenarios 2 and 3, based on total polygon area or private land area, respectively) or using combined private land and unsuitability as cost with ECAs as seeds (scenarios 10 and 11). The number of polygons selected in any scenario was exceeded by the number of polygons containing ECAs, but this number includes polygons that were less than 100% conserved. The percentage of the study area incorporated into candidate networks by scenarios ranged from 5 to 13%, compared to 12% in ECAs. The largest areas were required by scenarios based on combined private land and unsuitability with either ≥50%-conserved polygons as seeds (scenario 10; 13% of study area) or high spatial aggregation of polygons (scenario 13; 12% of study area). The smallest network was achieved by selecting only from suitable polygons without a spatial constraint (scenario 9; 5% of study area).

The equal costs and area-only scenarios (1 to 3) and private land area combined with unsuitability as cost with spatial aggregation (scenarios 12 and 13) produced conservation networks with the smallest percentages of area that was rated suitable (6–21%; Table 2). These scenarios also incorporated very small percentages of the suitable area that was available (4–15%). When unsuitability was the sole cost criterion or was combined with area without additional restrictions on selection (scenarios 4–8), only about one-third (29–34%) of the area selected was rated suitable. Similar percentages of suitability were obtained using ECA seeds in scenarios 10 and 11 (37 and 32%, respectively). In these scenarios, many unsuitable polygons were selected to meet goals for cover-type representation. Restricting selection to suitable polygons only with and without spatial constraint (scenarios 9, 14, and 15) ensured suitability (100%) and selected the highest percentage of available suitable area (54–73%). The other scenarios that incorporated unsuitability as a cost criterion (4–8, 10–13) selected less than one-third of the available suitable area, except scenario 10, in which the inclusion of many ECA-containing polygons as seeds increased the suitable area selected to 51% of available suitable area. A relatively high proportion of the suitable area available in the ICRB (49%) has been incorporated into ECAs. However, only 41% of ECAs were rated as suitable for conservation.

Among unsuitability-based scenarios without seeds or aggregation (4–8), scenario 4, using private land and unsuitability as costs in a 1 to 1 ratio, had the smallest area selected, smallest mean polygon size, largest area that was suitable, and largest available suitable area selected (Table 2). These characteristics led to the selection of this cost measure for the seed and aggregation scenarios. Scenarios 5 and 6, using total polygon area and unsuitability in 2 to 1 and 1 to 1 ratios, respectively, were similar to scenario 4 in network and mean polygon size, but had smaller suitable areas. The scenarios in which the weight of unsuitability exceeded that of area or was the only cost (7 and 8, respectively) were larger in network and mean polygon size than scenarios 4 to 6. Incorporation of seeds in scenario 4 (scenarios 10 and 11) increased the number of polygons and total area, decreased polygon size, and for scenario 10, increased the area that was suitable and available suitable area selected. Addition of moderate and high spatial aggregation to scenario 4 (scenarios 12 and 13, respectively) increased area selected, while greatly decreasing area that was suitable and available suitable area selected; mean polygon size increased with moderate aggregation (scenario 12), but decreased with high aggregation (scenario 13).

The geographic distributions of polygons selected in the scenarios reflected in part the differing locations of polygons of different sizes; i.e., the occurrence of larger polygons in areas with lower topographic relief in the Columbia Plateau of eastern Washington, eastern Oregon, and the Snake River plain of southern Idaho, and the occurrence of smaller polygons in mountainous regions such as the Cascades on the western edge of the study area, and the Rocky Mountains on the eastern edge and in central Idaho (Figs. 1a and 2). When cost was equal among polygons (scenario 1), large polygons with unsuitable ratings in the northwest, south-central, and southeast portions of the study area were selected for the diversity of grassland and shrubland cover types they contained (Fig. 5a). In contrast, use of area as cost (scenario 2) produced a network of many small polygons scattered throughout the study area except in those areas containing only relatively large polygons (Fig. 5b). Many small polygons were also selected when private land was used as cost (scenario 3), but a greater percentage of these polygons was suitable than was found in scenarios 1 and 2, as a result of inclusion of more public land in this network, especially wilderness areas in central Idaho (Fig. 5c).

The geographic distributions of suitable and unsuitable polygons were similar among scenarios incorporating unsuitability as part or all of cost without additional constraints (4 to 8), including selection of large, unsuitable polygons in the northern and western portions of the study area, and (mostly) suitable polygons in the southern and eastern portions (Fig. 5d–h). The distributions of polygons for scenarios 10 and 11, with ECA seed constraints (Fig. 5j, k), were broadly similar to other unsuitability scenario distributions, but included many additional polygons containing ECAs in the Rocky Mountains (eastern edge) and central and south-central portions of the study area. The effect of including moderate spatial aggregation with scenario 4 (scenario 12) was to reduce the number of suitable polygons in central Idaho, substituting larger polygons with reduced boundary length in the northwest and south-central portions of the study area that were rated unsuitable (Fig. 5l). The high aggregation scenario (13) produced a large cluster of suitable and unsuitable polygons in the south-central portion of the study area (Fig. 5m). The restriction of scenario 9 to suitable-only polygons concentrated the selected network in the southern and eastern portions of the study area where suitable polygons occurred (Fig. 5i). Spatial aggregation of suitable-only polygons (scenarios 14 and 15) did not result in dramatic differences in distribution from that of scenario 9 (Fig. 5n, o).

Fig. 5 Suitability ratings of polygons in study area for network selection scenarios, ranging from 1, most suitable (darkest gray), to –1, least suitable (lightest gray). (**a**) Equal costs; (**b**) total polygon area as cost; (**c**) private land area in polygon as cost; (**d**) private land and unsuitability as cost in 1 to 1 ratio; (**e**) total area and unsuitability as cost in 2 to 1 ratio; (**f**) total area and unsuitability as cost in 1 to 1 ratio; (**g**) total area and unsuitability as cost in 1 to 2 ratio; (**h**) unsuitability as cost; (**i**) unsuitability as cost, selecting from suitable polygons only; 1 (**j**) scenario 4 with polygons at least 50% conserved as seeds; (**k**) scenario 4 with 100% conserved polygons as seeds; (**l**) scenario 4 with boundary length modifier = 1; (**m**) scenario 4 with boundary length modifier = 10; (**n**) scenario 9 with boundary length modifier = 1; (**o**) scenario 9 with boundary length modifier = 10
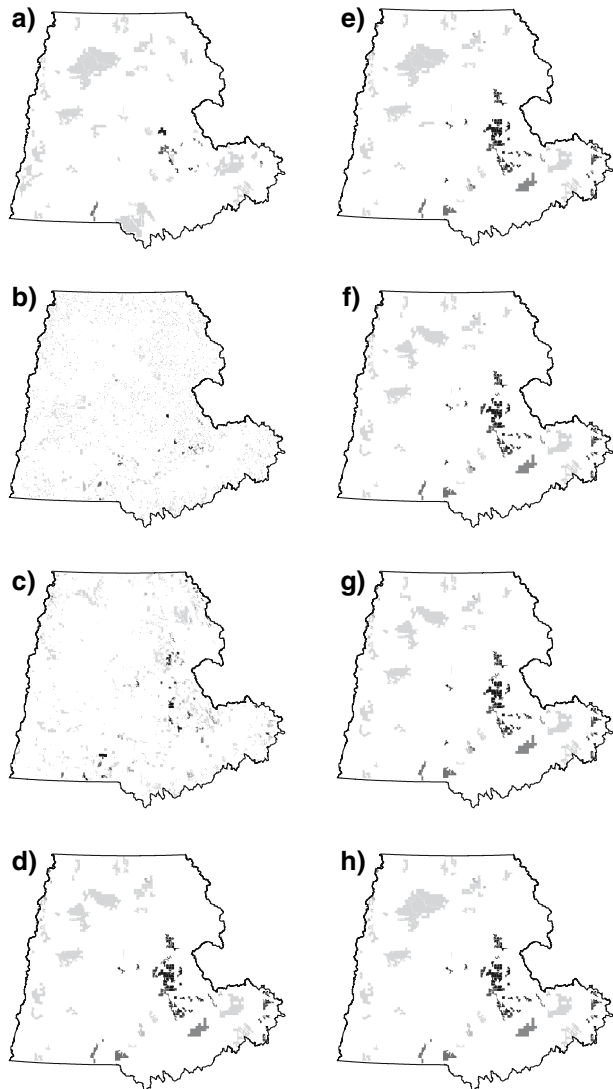
Spatial congruence of polygons selected in scenarios

Spatial congruence, expressed as the percentage of area occupied by polygons in common among networks, varied greatly among scenarios and ECAs (Table 3a). The area-only scenarios (2 and 3) had the lowest congruence percentages (1–25%) with other scenarios and ECAs, confirming the geographic distinctness of these networks (Fig. 5). Scenario 3, private land as cost, had its greatest congruence (25%) with scenario 10 (≥50%-conserved as seeds) and ECAs, primarily as a result of public lands occurring in all three networks. The high degree of spatial congruence (86 to 98%) among scenarios 4–8, incorporating unsuitability as a cost without additional restrictions on selection, reflected only small differences in the set of polygons comprising these networks. Congruence was also fairly

Fig 5 continued
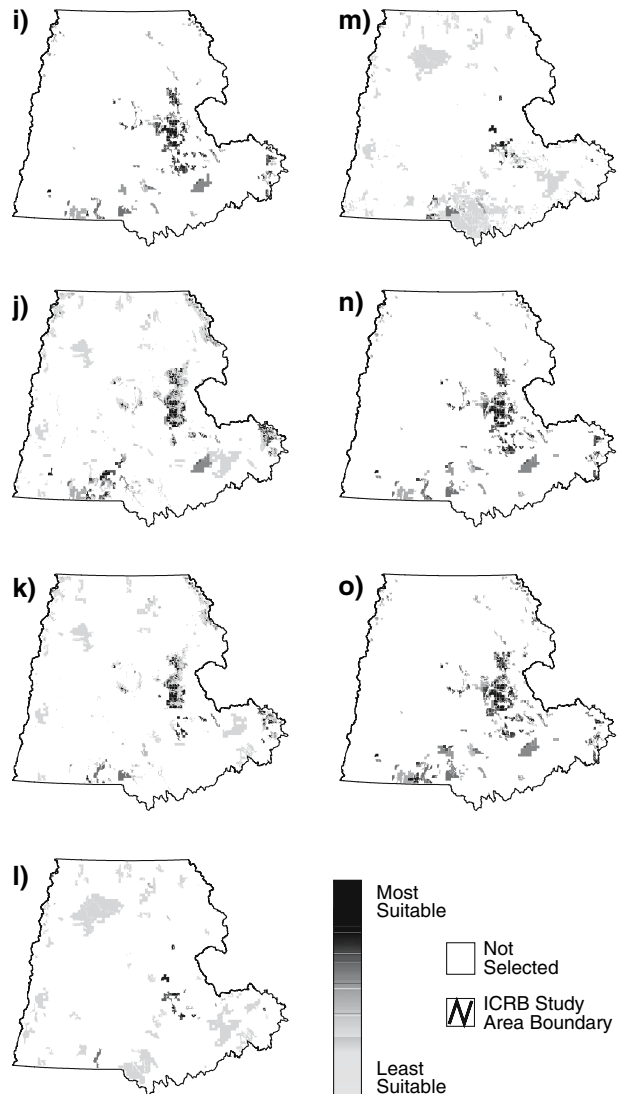
high (69–74%) between this group of scenarios and the equal costs scenario (1), due primarily to a shared set of large polygons rich in grassland and shrubland cover types but rated unsuitable. Moderate congruence (39–58%) was observed between scenarios 4–8 and the ECA-seed scenarios (10 and 11), as a result of a shared cost criterion, unsuitability, mitigated by the presence of ECA-containing polygons in the seed networks that were not included in scenarios 4–8. Similarly, scenarios 4–8 showed moderate overlap (41–59%) with the spatial aggregation scenarios based on scenario 4 (scenarios 12 and 13). Scenario 9, suitable-only polygons, had low to moderate overlap (maximum of 53%) with most other networks because of the presence of unsuitable polygons in these networks, but had high overlap (94–96%) with the spatial aggregation scenarios that were based on this scenario (scenarios 14 and 15), which were also highly congruent with each other. Scenario

Table 3 Percentage spatial congruence of polygon area among networks, i.e., area in common among pairs of scenarios and ECAs, calculated as (congruent area/row scenario area)*100

Scenario	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	ECAs
(a) Percentage total congruent area																
1	–	0.9	2.9	57.4	57.7	57.8	68.2	67.6	4.6	20.6	34.0	72.2	53.0	4.5	4.3	7.3
2	1.6	–	17.0	1.3	1.3	1.3	1.4	1.3	2.9	14.1	10.0	1.8	10.1	3.6	4.5	15.4
3	4.3	14.0	–	6.1	5.5	5.8	5.4	5.7	12.5	25.1	13.7	4.3	11.2	13.1	15.2	24.5
4	68.6	0.9	4.9	–	96.7	97.4	94.8	96.8	33.7	43.8	57.8	54.3	40.8	32.9	31.2	20.0
5	69.0	0.9	4.4	96.6	–	97.9	95.7	95.7	32.4	43.1	58.2	54.3	41.3	31.5	29.8	19.5
6	68.7	0.9	4.7	96.9	97.4	–	95.8	97.4	32.8	42.8	56.6	54.5	41.6	32.0	30.3	19.0
7	73.6	0.9	3.9	85.5	86.4	86.8	–	97.8	28.8	38.5	50.2	58.7	47.7	28.1	26.5	17.0
8	72.7	0.8	4.2	87.1	86.2	88.1	97.5	–	29.8	38.9	50.8	58.7	47.9	29.0	27.5	17.5
9	8.7	3.0	15.9	53.0	50.9	51.8	50.2	52.0	–	52.7	38.5	13.1	18.7	95.9	94.1	47.9
10	15.2	5.8	12.5	27.1	26.7	26.6	26.4	26.7	20.8	–	50.8	24.2	23.2	22.5	27.6	65.4
11	37.5	6.2	10.2	53.4	53.8	52.5	51.3	52.1	22.6	75.8	–	28.8	21.3	23.6	26.3	55.9
12	71.9	1.0	2.9	45.2	45.3	45.6	54.2	54.3	6.9	32.5	26.0	–	72.4	6.6	5.9	8.5
13	43.1	4.6	6.2	27.7	28.1	28.4	35.9	36.2	8.1	25.5	15.7	59.2	–	7.8	8.1	12.7
14	7.6	3.4	14.8	46.1	44.3	45.1	43.6	45.3	85.7	51.1	35.8	11.1	16.1	–	96.6	47.6
15	5.9	3.4	14.2	35.9	34.4	35.1	33.9	35.2	69.0	51.3	32.8	8.2	13.8	79.3	–	48.8
ECAs	6.0	7.1	13.7	13.8	13.5	13.2	13.0	13.5	21.1	73.1	41.9	8.3	13.8	21.8	23.5	–
(b) Percentage suitable congruent area																
1	–	10.5	11.5	73.5	73.5	73.5	73.5	73.5	81.3	12.4	28.1	85.3	52.6	79.9	75.0	39.7
2	16.1	–	23.8	19.2	19.2	19.2	19.2	19.2	43.7	33.8	33.1	7.1	32.9	54.7	66.9	43.3
3	4.5	6.1	–	26.3	23.5	24.2	22.5	24.9	58.5	65.9	37.8	11.2	17.4	61.2	71.1	61.5
4	14.7	2.5	13.4	–	94.2	95.1	92.3	97.7	99.3	59.1	55.3	22.5	25.0	96.8	91.8	52.9
5	15.3	2.6	12.5	97.9	–	97.4	96.0	95.6	99.3	59.5	56.2	23.4	24.7	96.7	91.5	53.7
6	15.0	2.6	12.6	97.1	95.8	–	94.6	97.3	99.3	57.6	53.5	23.0	24.3	96.7	91.6	51.2
7	15.5	2.7	12.1	97.4	97.4	97.6	–	97.3	99.3	58.4	53.7	23.8	25.6	96.6	91.3	52.1
8	14.9	2.6	12.9	99.5	93.6	97.0	93.9	–	99.3	58.4	54.8	23.0	25.4	96.8	91.7	52.2
9	8.7	3.0	15.9	53.0	50.9	51.8	50.2	52.0	–	52.7	38.5	13.1	18.7	95.9	94.1	47.9
10	1.4	2.5	18.9	33.3	32.2	31.7	31.1	32.3	55.6	–	44.0	4.1	9.5	60.3	73.8	80.3
11	5.5	4.2	18.7	53.8	52.5	50.9	49.6	52.3	70.2	76.1	–	9.3	17.1	73.2	81.5	75.6
12	63.4	3.5	21.1	83.8	83.8	83.8	83.8	83.8	91.2	27.0	35.6	–	62.5	86.4	77.5	41.1
13	21.5	8.8	18.1	51.0	48.5	48.5	49.6	51.0	71.6	34.4	36.0	34.4	–	69.0	71.8	45.6
14	7.6	3.4	14.8	46.1	44.3	45.1	43.6	45.3	85.7	51.1	35.8	11.1	16.1	–	96.6	47.6
15	5.9	3.4	14.2	35.9	34.4	35.1	33.9	35.2	69.0	51.3	32.8	8.2	13.8	79.3	–	48.8
ECAs	4.6	3.3	18.1	30.6	29.9	29.0	28.6	29.7	52.0	82.7	45.0	9.5	30.6	53.6	57.8	–

Scenarios as in Table 2; ECAs, existing conservation areas

10, ≥50%-conserved as seeds, and ECAs had low congruence (6–28%) with most other scenarios except each other and the other seed scenario (11) due to the presence of conserved lands in these networks that were not selected in the scenarios lacking seed constraints. For the same reason, scenario 11 (100%-conserved as seeds) achieved moderate overlap with other unconstrained unsuitability-based scenarios (4–8; overlap of 52–54%). Scenarios 12 and 13 had low to moderate overlap (1–54%) with most other scenarios

due to the inclusion of polygons to minimize boundary length that were not present in other scenarios except the equal costs scenario (1).

Patterns of spatial congruence in suitable polygon area were largely similar to those for total polygon area for most scenarios (Table 3b). The most striking difference was an increase in suitable area overlap of scenarios 1–8 and 10–13 with the suitable-only scenarios (9, 14, and 15) due to the incorporation of shared suitable polygons, but also the inclusion of polygons rated unsuitable in scenarios 1–8 and 10–13. In addition, most scenarios exhibited lower overlap in suitable area than total area with scenario 1, as a result of the very small suitable area included in this scenario.

Representation of cover-type targets in scenarios

Scenarios and ECAs varied widely in meeting requirements for area of cover types, including failure to represent some cover types (Table 4). Scenarios 3, 10, and 11 omitted the rarest cover type, Sierra Nevada mixed conifer, but this cover type was found in only one polygon, and covered only 2 km² in the study area. Occurrence in a single polygon meant that this cover type was either over-represented if the polygon was selected (100% of its area selected, rather than its target of 20%), or not represented if the polygon was not included in a network. ECAs did not contain Sierra Nevada mixed conifer or the second rarest cover type, Oregon white oak. In addition to omitting these two cover types, scenarios 9, 14, and 15 also failed to include cottonwood-willow and Pacific ponderosa pine because these four cover types did not occur in any polygons rated suitable.

Scenario 2, total area as cost, represented cover types most accurately, producing a network in which all cover types except Sierra Nevada mixed conifer were included at or very close to their desired target area (i.e., the proportion of the target area represented was at or near 1) (Table 4). This was an expected result because selection of small polygons to minimize total network size resulted in the ability of the algorithm to precisely meet targets without over-representation. Using private land as cost (scenario 3) also represented most cover types at or near their targets, but over-represented (i.e., proportion of target area > 1) several cover types, such as Engelmann spruce-subalpine fir and shrub or herb/tree regeneration.

Scenarios 4–8, incorporating unsuitability as a cost, adequately represented most cover types, but also over-represented some cover types (e.g., Engelmann spruce-subalpine fir, shrub or herb/tree regeneration, *Agropyron* bunchgrass, and mountain big sage; Table 4). A notable exception was the cover type shrub wetlands, which was consistently under-represented (i.e., proportion of target area < 1) due to its occurrence predominantly in polygons rated as unsuitable. In general, representation of cover types was similar among these five scenarios, as well as in the moderate spatial aggregation scenario (12). Scenario 12 also included over-representation of mountain big sagebrush, low sage, and shrub wetlands. Selection from suitable polygons only (scenario 9) produced a network with the greatest proportion of under-represented cover types due to their occurrence primarily in unsuitable areas. Representation of cover types was similar in scenarios 14 and 15, which added spatial aggregation to scenario 9, but over-representation of some cover types was increased, especially in scenario 15 (high aggregation). Scenarios incorporating ECAs as network seeds (10 and 11) were characterized by their over-representation of many cover types while meeting most target areas. Scenario 13 (high spatial aggregation) also over-represented many cover types while meeting most targets, but omitted Sierra Nevada mixed conifer and under-represented native forb.

Table 4 Proportion of 35 naturally-vegetated cover type target areas, effectiveness, efficiency, and fraction of area selected that was rated suitable (fraction suitable) of scenarios and existing conservation areas

Cover type	Target area (km²)	Scenario															ECAs
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Big sagebrush	4,695.3	0.92	1.00	1.00	1.09	1.32	1.07	1.07	1.34	1.17	2.91	0.78	1.10	1.18	1.25	1.41	2.74
Interior ponderosa pine	2,898.8	1.02	1.00	1.03	1.00	1.00	1.00	1.00	0.99	0.63	1.23	1.00	0.93	0.95	0.65	0.67	1.33
Interior Douglas fir	2,186.2	0.99	1.00	1.21	0.94	1.00	1.00	0.99	1.00	1.00	2.52	1.73	1.01	1.02	1.00	1.02	2.41
Lodgepole pine	1,931.6	1.01	1.00	1.47	1.18	1.13	1.17	1.12	1.20	1.42	4.42	3.08	1.00	1.02	1.47	1.66	4.39
Fescue-bunchgrass	1,505.3	0.99	1.00	1.00	0.88	0.88	0.93	0.87	0.90	0.94	1.00	0.98	0.98	0.81	1.00	1.00	1.04
Grand fir-white fir	1,414.5	1.14	1.00	1.15	1.25	1.12	1.16	1.14	1.10	0.64	1.81	1.33	1.00	1.02	0.64	0.66	1.59
Mountain big sage	1,412.5	3.11	1.00	1.40	1.22	1.21	1.20	1.23	1.21	1.60	1.11	1.52	3.04	3.07	1.66	1.75	2.39
Shrub or herb/tree regeneration	1,356.2	1.47	1.00	1.76	1.33	1.51	1.43	1.37	1.40	1.68	2.74	1.99	1.12	1.27	1.77	1.80	2.86
Western larch	1,352.4	0.99	1.00	1.00	1.00	1.00	1.00	0.95	1.00	0.24	0.96	0.98	0.98	0.98	0.25	0.26	0.44
Juniper-sagebrush	1,226.1	0.92	1.00	1.00	0.90	0.90	0.90	0.90	0.90	0.16	1.07	0.96	1.00	1.01	0.18	0.18	0.47
Engelmann spruce-subalpine fir	1,204.2	0.99	1.00	1.84	1.91	1.70	1.81	1.70	1.88	2.62	7.54	5.02	1.10	0.99	2.78	3.17	7.59
Low sage	1,098.4	3.09	1.00	1.00	0.91	1.00	1.00	1.01	0.91	1.02	1.56	1.03	2.90	3.17	1.06	1.19	1.81
Agropyron bunchgrass	1,008.3	1.40	1.00	1.00	1.28	1.28	1.28	1.28	1.28	0.23	0.90	0.40	0.73	0.81	0.23	0.24	0.76
Aspen	951.0	1.02	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.93	1.01	1.00	0.99	1.00	0.93	0.96	0.72
Salt desert shrub	849.8	0.96	1.00	1.00	0.79	0.96	0.96	0.96	0.79	1.30	2.75	1.28	0.61	0.96	1.36	1.47	3.18
Whitebark pine	835.6	0.80	1.00	1.00	0.69	0.68	0.67	0.67	0.69	0.90	1.66	1.18	0.69	0.66	1.00	1.00	1.87
Western red cedar-western hemlock	755.6	0.90	1.00	1.00	0.95	0.97	0.97	1.00	0.97	0.27	0.92	1.00	0.98	0.99	0.27	0.27	0.30
Mixed conifer woodlands	559.8	0.75	1.00	0.98	0.84	0.69	0.89	0.84	0.75	0.01	0.71	0.83	0.87	0.89	0.01	0.01	0.06
Mountain mahogany	404.8	0.83	1.00	1.00	0.80	0.80	0.80	0.80	0.80	0.17	0.68	0.78	0.86	0.86	0.18	0.19	0.12
Shrub wetlands	295.6	0.29	1.00	0.88	0.17	0.17	0.17	0.17	0.17	0.10	0.47	0.23	0.17	2.54	0.10	0.09	0.54
Pacific silver fir-mountain hemlock	295.6	0.49	1.00	1.00	0.93	0.82	0.93	0.93	0.82	0.76	2.31	1.49	0.69	0.74	0.76	0.78	2.41
Mountain hemlock	217.0	0.86	1.00	0.98	0.90	0.90	0.90	0.89	0.90	0.23	1.17	0.93	0.85	0.92	0.23	0.24	1.04

Table 4 continued

Cover type	Target area (km²)	Scenario															ECAs
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Antelope bitterbrush-bluebunch wheatgrass	213.2	1.12	1.00	1.00	0.86	1.11	0.86	1.02	1.11	0.05	0.91	0.99	1.16	1.21	0.05	0.05	0.17
Pacific ponderosa pine	212.0	1.01	1.00	0.81	1.01	1.02	1.01	1.01	1.01	0.00	0.90	0.81	0.90	0.90	0.00	0.00	0.19
Herbaceous wetlands	187.4	1.13	1.00	0.91	1.00	1.02	1.02	1.02	1.00	0.21	1.09	1.00	0.94	1.14	0.22	0.22	0.15
Juniper woodlands	167.0	0.91	1.01	0.84	0.82	0.84	0.84	0.84	0.82	0.36	0.92	0.78	0.86	0.99	0.36	0.38	0.68
Alpine tundra	125.0	0.97	1.00	0.96	0.96	0.94	0.95	0.96	0.95	1.24	3.36	2.32	0.73	0.90	1.26	1.17	3.40
Western white pine	92.4	1.06	1.00	1.01	0.88	0.85	0.88	0.88	0.85	0.34	1.00	0.94	0.77	0.93	0.34	0.34	0.67
Limber pine	56.2	0.75	1.00	1.62	0.57	0.53	0.53	0.53	0.57	0.60	0.37	0.37	0.94	0.87	0.62	0.66	0.04
Chokecherry-serviceberry-rose	37.8	1.19	1.01	1.01	1.03	1.01	1.03	1.03	1.01	0.03	1.35	1.01	1.51	1.69	0.03	0.03	0.48
Cottonwood-willow	20.8	1.30	0.96	1.01	1.30	1.30	1.30	1.30	1.30	0.00	1.06	1.30	1.30	1.30	0.00	0.00	0.10
Whitebark pine-alpine larch	16.4	0.98	1.04	1.22	1.04	1.04	1.04	1.04	1.04	0.12	1.22	1.52	1.04	1.04	0.12	0.12	1.40
Native forb	9.6	0.94	0.83	0.63	0.94	0.94	0.83	0.94	0.52	0.21	0.94	0.83	0.73	0.73	0.21	0.21	0.31
Oregon white oak	8.0	3.13	1.13	1.13	3.13	1.13	3.13	3.13	3.13	0.00	1.13	1.13	3.13	3.13	0.00	0.00	0.00
Sierra Nevada mixed conifer	0.4	5.00	5.00	0.00	5.00	5.00	5.00	5.00	5.00	0.00	0.00	0.00	5.00	5.00	0.00	0.00	0.00
Effectiveness	–	0.92	0.99	0.94	0.91	0.91	0.92	0.92	0.89	0.49	0.90	0.87	0.89	0.94	0.50	0.50	0.63
Efficiency	–	0.90	0.95	0.93	0.92	0.91	0.92	0.92	0.91	0.95	0.87	0.91	0.91	0.92	0.95	0.94	0.88
Fraction suitable	–	0.06	0.07	0.21	0.34	0.33	0.33	0.29	0.30	1.00	0.37	0.32	0.08	0.11	1.00	1.00	0.41

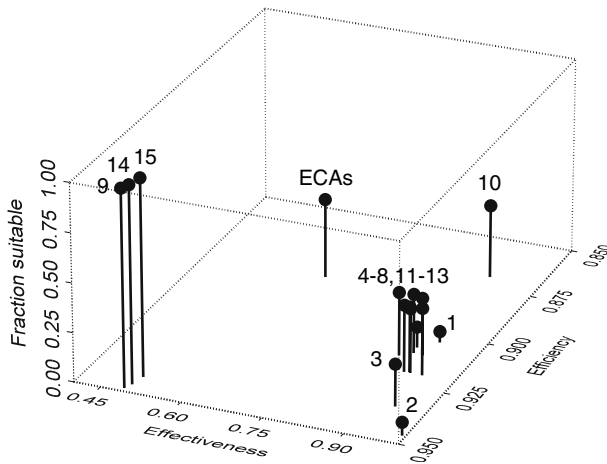Scenarios as in Table 2; ECAs, existing conservation areas

Fig. 6 Relationships of scenario effectiveness, efficiency, and fraction suitable. Scenarios: 1, equal costs; 2, total polygon area as cost; 3, private land area in polygon as cost; 4, private land and unsuitability as cost in 1 to 1 ratio; 5, total area and unsuitability as cost in 2 to 1 ratio; 6, total area and unsuitability as cost in 1 to 1 ratio; 7, total area and unsuitability as cost in 1 to 2 ratio; 8, unsuitability as cost; 9, unsuitability as cost, selecting from suitable polygons only; 10, scenario 4 with polygons at least 50% conserved as seeds; 11, scenario 4 with 100% conserved polygons as seeds; 12, scenario 4 with boundary length modifier = 1; 13, scenario 4 with boundary length modifier = 10; 14, scenario 9 with boundary length modifier = 1; 15, scenario 9 with boundary length modifier = 10

ECAs varied widely in representation, as expected, because our cover-type target areas played no role in their selection (Table 4). ECAs contained varying percentages of total cover-type area in the ICRB, ranging from no area (Sierra Nevada mixed conifer and Oregon white oak) to 82% of area for alpine tundra, and averaging 19% represented (Bourgeron et al. to be submitted).

Effectiveness, efficiency, and suitability of scenarios and ECAs

The three measures that we used to evaluate the performance of scenarios and ECAs (effectiveness in representing cover type targets, efficiency in minimizing network area, and the fraction of area selected that was rated suitable or fraction suitable) ranged from 0 (worst performance) to 1 (best performance). Most scenarios were reasonably effective and efficient; fraction suitable varied most widely among the three measures (Table 4, Fig. 6). The highest effectiveness value was obtained for scenario 2, area as cost (0.99); the lowest values occurred in scenarios 9, 14, and 15 (0.49–0.51), selecting from suitable polygons only, and ECAs (0.63). Other scenarios ranged in effectiveness from 0.87 to 0.94. Efficiency values were highest (0.93–0.95) for the suitable-only scenarios and the area-as-cost scenarios (0.95 and 0.93 for scenarios 2 and 3, respectively). Equal costs, unsuitability as part or all of cost, and 100%-conserved polygons as seeds (scenarios 1, 4–8, and 11, respectively) produced networks with slightly lower efficiency values (0.90–0.92). The lowest efficiency values were obtained for the ≥ 50%-conserved seed scenario (10) and ECAs (0.87 and 0.88, respectively). The fraction suitable was lowest for scenarios 1, 2, 12, and 13 (0.06–0.11), highest for scenarios 9, 14, and 15 (1.00), and intermediate (0.21–0.41) for all other scenarios and ECAs.

No network exhibited high values for all three measures (Table 4, Fig. 6). Scenario 2, area as cost, was highly effective and efficient, but had low suitable area. Scenarios 9, 14, and 15, selection from suitable polygons only, were suitable and efficient, but not effective. Scenario 10, ≥50%-conserved polygons as seeds, was effective and had a moderately high fraction suitable, but was the least efficient. Scenarios using unsuitability as part or all of cost (4–8 and 11) were effective and had intermediate efficiency and suitable area. Addition of spatial aggregation (scenarios 12 and 13) decreased both efficiency and fraction suitable.

Discussion and conclusions

The cost measures compared in the scenarios differed in their advantages and disadvantages for network selection. Ideally, measures of conservation network costs should reflect, at least in part, economic considerations such as prices of land acquisition and costs of foregone economic opportunities (Bedward et al. 1992; Stewart and Possingham 2005; Davis et al. 2006), but direct measures of such quantities are not usually available for large regions (see Ando et al. 1998 for use of county-level agricultural land values as costs). As a consequence, a number of network selection studies have used land area as a surrogate measure for land costs, targeting features ranging from species to land types, and using both optimizing and heuristic algorithms to make selections (Possingham et al. 2000; ReVelle et al. 2002; Davis et al. 2006). In our study, the use of polygon area as cost (scenario 2) selected a relatively small total area while precisely attaining the target areas of most cover types. However, the sheer number of polygons identified in this scenario and their spatial dispersion (because we did not constrain the algorithm to minimize boundary length) would be an impediment to conducting further (i.e., finer-scale) analyses. The unsuitability of nearly all this network indicates that additional difficulties could be expected in establishing viable conservation areas.

The use of private land area as a cost (scenario 3) focused selection on public lands, which lack acquisition costs, making such a network more economically achievable. In many cases, the ecological conditions of public lands may also be more compatible with conservation goals than privately-owned areas. However, inclusion of particular public land areas in conservation networks could require changes in management, including restoration, to sustain targets of conservation over time, and could involve a lengthy, politically difficult process in our study area.

In our study, the use of a cost derived from suitability ratings (alone and in combination with other constraints) incorporating ecological condition and socio-economic attributes, changed most characteristics of the network compared to the use of land area as cost (Tables 2–4; Figs. 5 and 6). Selecting only from polygons rated suitable (scenarios 9, 14, and 15) was most likely to produce a network that was viable and defensible, as represented in our knowledge-based system, as well as reasonably efficient. A drawback of this approach is the omission from the network of unsuitable land areas that may be the only sources for representing some cover-type targets, limiting the effectiveness of the network. Three of the cover types omitted from this network, Pacific ponderosa pine, Oregon white oak, and Sierra Nevada mixed conifer, occupy extensive areas to the west of our study area (Eyre 1980). However, even if these cover types are well-represented in conservation areas outside the study area, further investigation at a local scale would be needed to determine whether their inclusion in an ICRB conservation network would contribute to representing their full range of environmental variability, the loss of which could restrict future

opportunities for adaptation to changing environmental conditions. This also applies to cover types with low representation in the candidate networks.

The use of unsuitability as a cost criterion to select candidate conservation areas better met the targets for cover types (i.e., was more effective) than restriction to suitable polygons only as a cost criterion. However, effectiveness was improved at the cost of including unsuitable land in the network because some cover types were present only in areas rated unsuitable. Even when unsuitability was combined with private land to determine cost, focusing selection on suitable public lands, the networks included some large polygons that contained private land, as well as human-modified cover types that were not targets of conservation.

In addition to the cost measures already mentioned (land price, land area, and unsuitability), other measures of the costs of acquiring and maintaining conservation networks should include ecosystem restoration and management to meet specific conservation goals (Reynolds and Hessburg 2005; Noss et al. 2006). Our use of unsuitability as a cost criterion does not directly address restoration or management costs. However, the indices of vegetation and disturbance regime change from historical conditions, which were evaluated in the viability component of the KB, constitute a qualitative characterization of the potential need for restoration activities. The demonstrated contribution of road density to determining the suitability of land areas for conservation (Humphries et al. in revision) also indicates the potential to restore particular areas by means of methods such as phasing out roads. Incorporation of land-management condition as a criterion for suitability also qualitatively characterizes the degree to which current management of federal lands is consistent with conservation goals. The addition of land-management condition for private land as a criterion would be useful.

Compact or aggregated reserve networks have the advantage of facilitating species migration and mitigating edge effects and fragmentation, but may also be more vulnerable to species loss resulting from large catastrophic disturbances and have lower species and environmental diversity than elongated or dispersed reserve networks (Shafer 2001; Cabeza et al. 2004; Williams et al. 2005; Van Teeffelen et al. 2006). The spatial aggregation scenarios exhibited a tradeoff between suitability and clustering of candidate sites due to the dispersed locations of areas that were rated suitable. It may not be possible to achieve a network that is both suitable and highly spatially aggregated by minimizing boundary length for the set of polygons, conservation targets, and suitability ratings in our study.

Many studies have identified a lack of efficiency in ECAs compared to conservation networks selected using optimizing or heuristic algorithms (e.g., 11 studies summarized in Rodrigues et al. 1999). In our study, although the efficiency of ECAs was lower than all but one scenario (10), the magnitude of the differences in efficiency between the scenarios and ECAs was relatively small. ECAs were less effective than all scenarios except 9, 14, and 15, which were based on selection from suitable-only polygons. Only two cover types were entirely omitted from ECAs, but seven of the cover types represented in ECAs contained less than 20% of the area targets we specified (Table 4). Most of these under-represented cover types occurred predominantly in areas rated as unsuitable, and were therefore also under-represented in the suitable-only scenarios. Cover types over-represented in ECAs tended to be those occurring at higher elevations in the study area (e.g., alpine tundra, Engelmann spruce-subalpine fir, lodgepole pine); such biases in favor of upland types unsuitable for agriculture and development have been reported in other studies (Pressey and Logan 1994; Scott et al. 2001). Although ECA suitability was greater than that of most scenarios, 59% of ECA-containing land area received a rating of unsuitable. This circumstance can be attributed to several factors, including assignment of

unsuitability ratings to polygons only partially occupied by ECAs, in which unsuitability derived from non-ECA conditions, such as high road densities or unfavorable human impacts in polygons or neighboring areas. The relatively coarse scale of the data layers evaluated to determine suitability (1 km^2 grid cell size) compared to the size of some conservation areas may have obscured some fine-scale differences in ecological conditions.

The lack of efficiency in networks generated using ECAs as seeds in scenarios 10 and 11 is in agreement with other studies in which networks were larger with ECAs than without them (Pressey et al. 1996); the mismatch in boundaries between ECAs and selection units is a contributing factor to this increase in network area (Rodrigues et al. 1999). Use of 100%-conserved polygons as seeds (scenario 11) did not result in improvement in effectiveness, efficiency, or suitability over other scenarios. Scenario 10, ≥50%-conserved as seeds, produced only a modest gain in suitability for its large increase in network size.

We view our results as indicative rather than prescriptive, and as possible starting points for further analyses of conservation networks stratified at both regional and local scales (Lombard et al. 1995; Davis et al. 1996; Pressey et al. 1996; Cowling et al. 1999; Stoms et al. 2002; Rouget 2003). Identification of likely candidate conservation areas at the regional level should be followed by finer-scale examination of these sites to minimize acquisition costs and concentrate conservation activities on confirmed cover-type locations in good condition. The unsuitability-based and suitability-only scenarios selected a manageable number of polygons on which additional conservation efforts could be focused. The tradeoffs we detected between suitability and effectiveness suggest that a multi-stage process could be implemented to address both attributes of candidate conservation networks (Stoms et al. 2002). Further adjustments of candidate site boundaries could be made based on fine-scale knowledge of suitability, locations of target features, and land uses, either through enhancing the suitability of unsuitability-based networks by removing locally unsuitable areas or enhancing suitable-only networks by adding areas containing needed targets. Explicit consideration of restoration costs, such as fire management and phasing out roads, is potentially important in conservation planning at a regional scale in cases where suitable conservation areas do not include all conservation targets.

References

Ahamed TRN, Rao KG, Murthy JSR (2000) GIS-based fuzzy membership model for crop-land suitability analysis. Agric Syst 63:75–95

Andelman S, Ball I, Davis F, Stoms D (1999) Sites V 1.0: an analytical toolbox for designing ecoregional conservation portfolios. Manual prepared for The Nature Conservancy. University of California, Santa Barbara

Ando A, Camm J, Polasky S, Solow A (1998) Species distributions, land values, and efficient conservation. Science 279:2126–2128

Baja S, Chapman DM, Dragovich D (2002) A conceptual model for defining and assessing land management units using a fuzzy modeling approach in GIS environment. Environ Manage 29:647–661

Bedward M, Pressey RL, Keith DA (1992) A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. Biol Conserv 62:115–125

Bourgeron PS, Humphries HC (in revision) Evaluating the performance of ecological land classifications: Do they represent variability in patterns central to conservation goals? Biol Conserv

Bourgeron PS, Humphries HC, Reynolds KM (2001) Representativeness assessments. In: Jensen ME, Bourgeron PS (eds) A guidebook for integrated ecological assessments. Springer, New York

Bourgeron PS, Humphries HC, Reynolds KM (to be submitted) A regional framework for evaluating the suitability of land areas for conservation. Biol Conserv

Braimoh AK, Pyke PLG, Stein A (2004) Land evaluation for maize based on fuzzy set and interpolation. Environ Manage 33:226–238

Brooks TM, da Fonseca GAB, Rodrigues ASL (2004) Protected areas and species. Conserv Biol 18:616–618

Cabeza M, Moilanen A (2001) Design of reserve networks and the persistence of biodiversity. Trends Ecol Evol 16:242–248

Cabeza J, Araújo MB, Wilson RJ, Thomas CD, Cowley MJR, Moilanen A (2004) Combining probabilities of occurrence with spatial reserve design. J Appl Ecol 41:252–262

Cowling RM, Pressey RL, Lombard AT, Desmet PG, Ellis AG (1999) From representation to persistence: requirements for a sustainable system of conservation areas in the species-rich Mediterranean-climate desert of southern Africa. Divers Distrib 5:51–71

Csuti B, Polansky S, Williams PH, Pressey RL, Camm JD, Kershaw M, Kiester AR, Downs B, Hamilton R, Huso M, Sahr K (1997) A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. Biol Conserv 80:83–97

Dai JJ, Lorenzato S, Rocke DM (2004) A knowledge-based model of watershed assessment for sediment. Environ Modell Softw 19:423–433

Davidson DA, Theocharopoulos SP, Bloksma RJ (1994) A land evaluation project in Greece using GIS and based on Boolean and fuzzy set methodologies. Int J Geogr Inf Syst 8:369–384

Davis FW, Costello C, Stoms D (2006) Efficient conservation in a utility-maximization framework. Ecol Soc 11:33 [online] URL: http://www.ecologyandsociety.org/vol11/iss1/art33

Davis FW, Stoms DM, Andelman S (1999) Systematic reserve selection in the USA: an example from the Columbia Plateau ecoregion. Parks 9:31–41

Davis FW, Stoms DM, Church RL, Okin WJ, Johnson NL (1996) Selecting biodiversity management areas. In: Sierra Nevada Ecosystem Project: final report to Congress, vol II. University of California, Centers for Water and Wildland Resources, Davis, pp 1503–1528

Eyre FH (ed) (1980) Forest cover types of the United States and Canada. Society of American Foresters, Washington, DC

Fairbanks DHK, Reyers B, van Jaarsveld AS (2001) Species and environment representation: selecting reserves for the retention of avian diversity in KwaZulu-Natal, South Africa. Biol Conserv 98:365–379

Fischer DT, Church RL (2005) The SITES reserve selection system: a critical review. Environ Model Assess 10:215–228

Gravenmier RA, Wilson AE, Steffenson JR (1997) Information system development and documentation. In: Quigley TM, Arbelbide SJ (eds) An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins, vol II. U.S. Department of Agriculture Forest Service General Technical Report PNW-GTR-405, Pacific Northwest Research Station, Portland, 2011–2067

Groenemans R, Van Ranst E, Kerre E (1997) Fuzzy relational calculus in land evaluation. Geoderma 77:283–298

Hall GB, Wang F, Subaryono (1992) Comparison of Boolean and fuzzy classification methods in land suitability analysis by using geographical information systems. Environ Plan A 24:497–516

Hann WJ, Jones JL, Karl MG, Hessburg PF, Keane RE, Long DG, Menakis JP, McNicoll CH, Leonard SG, Gravenmier RA, Smith BG (1997) Landscape dynamics of the Basin. In: Quigley TM, Arbelbide SJ (eds) An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins, vol II. U.S. Department of Agriculture Forest Service General Technical Report PNW-GTR-405, Pacific Northwest Research Station, Portland, 337–1055

Humphries HC, Bourgeron PS, Reynolds KM (in revision) The effect of data availability on the determination of suitability of land units for conservation using a knowledge-based system. Environ Modell Softw

Jensen M, Goodman I, Brewer K, Frost T, Ford G, Nesser J (1997) Biophysical environments of the basin. In: Quigley TM, Arbelbide SJ (eds) An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins, vol I. U.S. Department of Agriculture Forest

Service General Technical Report PNW-GTR-405, Pacific Northwest Research Station, Portland, 99–314

Kelley C, Garson J, Aggarwal A, Sarkar S (2002) Place prioritization for biodiversity reserve network design: a comparison of the SITES and ResNet software packages for coverage and efficiency. Divers Distrib 8:297–306

Kollias VJ, Kalivas DP (1998) The enhancement of a commercial geographical information system (ARC-INFO) with fuzzy processing capabilities for the evaluation of land resources. Comput Electron Agr 20:79–95

Lombard AT, Nicholls AO, August PV (1995) Where should nature reserves be located in South Africa? A snake's perspective. Conserv Biol 9:363–372

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253

Margules CR, Pressey RL, Williams PH (2002) Representing biodiversity: data and procedures for identifying priority areas for conservation. J Biosci 27:309–326

McDonnell MD, Possingham HP, Ball IR, Cousins EA (2002) Mathematical methods for spatially cohesive reserve design. Environ Model Assess 7:107–114

Nantel P, Bouchard A, Brouillet L, Hay S (1998) Selection of areas for protecting rare plants with integration of land use conflicts: a case study for the west coast of Newfoundland, Canada. Biol Conserv 84:223–234

Noss RF (1987) From plant communities to landscapes in conservation inventories: a look at The Nature Conservancy. Biol Conserv 41:11–37

Noss RF, Beier P, Covington WW, Grumbine RE, Lindenmayer DB, Prather JW, Schmiegelow F, Sisk TD, Vosick DJ (2006) Recommendations for integrating restoration ecology and conservation biology in ponderosa pine forests of the southwestern United States. Restor Ecol 14:4–10

Oetting JB, Knight AL, Knight GR (2006) Systematic reserve design as a dynamic process: F-TRAC and the Florida Forever program. Biol Conserv 128:37–46

Poiani KA, Richter BD, Anderson MG, Richter HE (2000) Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. BioScience 50:133–46

Possingham H, Ball I, Andelman S (2000) Mathematical methods for identifying representative reserve networks. In: Ferson S, Burgman M (eds) Quantitative methods for conservation biology. Springer-Verlag, New York, 291–305

Pressey RL (2004) Conservation planning and biodiversity: assembling the best data for the job. Conserv Biol 18:1677–1681

Pressey RL, Logan VS (1994) Level of geographic subdivision and its effects on assessments of reserve coverage: a review of regional studies. Conserv Biol 8:1037–1046

Pressey RL, Nicholls AO (1989) Efficiency in conservation evaluation-scoring versus iterative approaches. Biol Conserv 50:199–218

Pressey RL, Humphries CJ, Margules CR, Vane-Wright RI, Williams PH (1993) Beyond opportunism: key principles for systematic reserve selection. Trends Ecol Evol 8:124–128

Pressey RL, Possingham HP, Day JR (1997) Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. Biol Conserv 80:207–219

Pressey RL, Possingham HP, Margules CR (1996) Optimality in reserve selection algorithms: when does it matter and how much? Biol Conserv 76:259–267

Pyke CR (2005) Assessing suitability for conservation action: prioritization interpond linkages for the California tiger salamander. Conserv Biol 19:492–503

Quigley TM, Arbelbide SJ (eds) (1997) An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins, vol I. U.S. Department of Agriculture Forest Service General Technical Report PNW-GTR-405, Pacific Northwest Research Station, Portland

Ray D, Reynolds K, Slade J, Hodge S (1998) A spatial solution to ecological site classification for British forestry using Ecosystem Management Decision Support. In: Proceedings of the third international conference on geocomputation, Bristol, September 17–19, 1998, http://www.fsl.orst.edu/emds/geocomp/geopap3.html

Reid MS, Bourgeron PS, Humphries HC, Jensen ME (eds) (1995) Documentation of the modeling of potential vegetation at three spatial scales using biophysical settings in the Columbia River basin assessment area. URL: http://www.icbemp.gov/science/reid_1.pdf

ReVelle CS, Williams JC, Boland JJ (2002) Counterpart models in facility location science and reserve selection science. Environ Model Assess 7:71–80

Reynolds KM (1999a) EMDS users guide (version 2.0): knowledge-based decision support for ecological assessment. U.S. Department of Agriculture Forest Service General Technical Report PNW-GTR 470, Pacific Northwest Research Station, Portland

Reynolds KM (1999b) NetWeaver for EMDS version 2.0 users guide: a knowledge base development system. U.S. Department of Agriculture Forest Service General Technical Report PNW-GTR 471, Pacific Northwest Research Station, Portland

Reynolds KM (2001) Using a logic framework to assess forest ecosystems sustainability. J Forest 99:26–30

Reynolds KM, Hessburg PF (2005) Decision support for integrated landscape evaluation and restoration planning. For Ecol Manage 207:263–278

Reynolds KM, Jensen M, Andreasen J, Goodman I (2000) Knowledge-based assessment of watershed condition. Comput Electron Agr 27:315–334

Reynolds KM, Johnson KN, Gordon SN (2003) The science/policy interface in logic-based evaluation of forest ecosystem sustainability. Forest Policy Econ 5:433–446

Rodrigues ASL, Tratt R, Wheeler BD, Gaston KJ (1999) The performance of existing networks of conservation areas in representing biodiversity. P Roy Soc Lond B 266:1453–1460

Rouget M (2003) Measuring conservation value at fine and broad scales: implications for a diverse and fragmented region, the Agulhas Plain. Biol Conserv 112:217–232

Sarkar S, Pressey RL, Faith DP, Margules CR, Fuller T, Stoms DM, Moffett A, Wilson KA, Williams KJ, Williams PH, Andelman S (2006) Biodiversity conservation planning tools: present status and challenges for the future. Annu Rev Env Resour 31:123–159

Scott JM, Davis FW, McGhie RG, Wright RG, Groves C, Estes J (2001) Nature reserves: do they capture the full range of America's biological diversity? Ecol Appl 11:999–1007

Shafer CL (2001) Inter-reserve distance. Biol Conserv 100:215–227

Sicat RS, Carranza EJM, Nidumolu UB (2005) Fuzzy modeling of farmers' knowledge for land suitability. Agric Syst 83:49–75

Snyder SA, Tyrrell LE, Haight RG (1999) An optimizing approach to selecting Research Natural Areas in National Forests. Forest Sci 45:458–469

Stewart RR, Possingham HP (2005) Efficiency, costs and trade-offs in marine reserve system design. Environl Model Assess 10:203–213

Stoms DM, Borchert MI, Moritz MA, Davis FW, Church RL (1998) A systematic process for selecting representative research natural areas. Nat Area J 18:338–349

Stoms DM, McDonald JM, Davis FW (2002) Fuzzy assessment of land suitability for scientific research reserves. Environ Manage 29:545–558

Triantafilis J, Ward WT, McBratney AB (2001) Land suitability assessment in the Namoi Valley of Australia, using a continuous model. Aust J Soil Res 39:273–290

USDA Forest Service (1992) Preparing for the future: Forest Service research natural areas. FS-503

Van Langevelde F, Schotman A, Claassen F, Sparenburg G (2000) Competing land use in the reserve site selection problem. Landscape Ecol 15:243–256

Van Ranst E, Tang H, Groenemans R, Sinthurahat S (1996) Application of fuzzy logic to land suitability for rubber production in peninsular Thailand. Geoderma 70:1–19

Van Teeffelen AJA, Cabeza M, Moilanen A (2006) Connectivity, probabilities and persistence: comparing reserve selection strategies. Biodiv Conserv 15:899–919

Wessels KJ, Freitag S, Van Jaarsveld AS (1999) The use of land facets as biodiversity surrogates during reserve selection at a local scale. Biol Conserv 89:21–38

Wessels KJ, Reyers B, Van Jaarsveld AS (2000) Incorporating land cover information into regional biodiversity assessments in South Africa. Anim Conserv 3:67–79

Westphal MI, Possingham HP (2003) Applying a decision-theory framework to landscape planning for biodiversity: follow-up to Watson et al. Conserv Biol 17:327–329

Williams PH (1998) Key sites for conservation: area-selection methods for biodiversity. In: Mace GM, Balmford A, Ginsberg JR (eds) Conservation in a changing world. Cambridge University Press, Cambridge, 269–287

Williams JC, ReVelle CS, Levin SA (2004) Using mathematical optimization models to design nature reserves. Front Ecol Environ 2:98–105

Williams JC, ReVelle CS, Levin SA (2005) Spatial attributes and reserve design models: a review. Environ Model Assess 10:163–181